




Effects of early life mass mortality events on fish populations

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Abstract

Mass mortality events are ubiquitous in nature and can be caused by, for example, diseases, extreme weather and human perturbations such as contamination. Despite being prevalent and rising globally, how mass mortality in early life causes population-level effects such as reduced total population biomass, is not fully explored. In particular for fish, mass mortality affecting early life may be dampened by compensatory density-dependent processes. However, due to large variations in year-class strength, potentially caused by density-independent variability in survival, the impact at the population level may be high in certain years. We quantify population-level impacts at two levels of mass mortality (50% and 99% additional mortality) during early life across 40 fish species using age-structured population dynamics models. The findings from these species-specific models are further supported by an analysis of detailed stock-specific models for three of the species. We find that population impacts are highly variable between years and species. Short-lived species that exhibit a low degree of compensatory density dependence and high interannual variation in survival experience the strongest impacts at the population level. These quantitative and general relationships allow predicting the range of potential impacts of mass mortality events on species based on their life history. This is critical considering that the frequency and severity of mass mortality events are increasing worldwide.

KEYWORDS

early life, fish, life history, mass mortality events, population level

1 | INTRODUCTION

Mass mortality events, often defined as events with a 50% decline in abundance over a short period (<1 year, cf., Reed et al., 2003), can be caused by, for example, disease outbreaks, extreme weather, thermal stress and anthropogenic activities (Fey et al., 2015). Recently, a global increase in the occurrence of mass mortality events has been reported across taxa, including birds, fish, mammals, reptiles, amphibians and invertebrates (Fey et al., 2015). The short time-scale and large impact of mass mortality events can have important

ecological consequences, directly through depressed population level biomass or indirectly through effects in the ecosystem. Mass mortality events will often directly affect certain age classes, sizes or life stages of organisms. In particular, for fish, mass mortality events have been reported at the adult stage (Ohlberger et al., 2011) and at the early life stages, such as at the egg or larval (Rooper et al., 2013; Vikebø et al., 2014) and juvenile stages (Gjøsæter et al., 2000). The survival of the early life stages of fish tends to be particularly affected by external perturbations. Mortality events in these stages may be caused by various stressors, including anthropogenic

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environmental contamination (Incardona et al., 2014), biotoxicity (Chan et al., 2003; Gjørseter et al., 2000) and climate-related events such as ocean warming (Dahlke et al., 2020; Rogers et al., 2021) and storms (Lough et al., 1996).

However, population-level consequences of mass mortality events at the early life stage in fish are highly uncertain as natural mortality is also high and variable in these life stages. The population-level consequences will likely depend on a range of factors, such as mean and interannual variability in fecundity, survival and growth as well as the degree of density-dependent regulation (Vincenzi et al., 2014). For example, we expect an early life stage mass mortality event to have a stronger effect at the population level in a short-lived species compared to long-lived species (Reed et al., 2003). Moreover, if the interannual variance in year-class strength (i.e. the egg production weighted with consecutive survival) is high, we generally expect the effect at the population level to be low if the mass mortality event affects a weak year-class and high if the mass mortality affects a strong year-class. In contrast, in a situation where variance in year class strength is low, we expect the effects at the population level to be similar across years. Finally, compensatory density dependence in survival will dampen the effects of mortality events due to increased survival probability at low density. Hence, population-level effects of early-life mass mortality will typically be larger if compensatory density dependence in survival is weak.

Anthropogenically driven mass mortality events may be of particular concern and marine oil spills are one such example that can have severe detrimental impacts on the marine environment (Jernelöv, 2010; Langangen, Olsen, et al., 2017; Peterson et al., 2003). Oil components such as Polycyclic Aromatic Hydrocarbons (PAHs) particularly affect early life stages of fish at the individual level through malformations, for example, cardiovascular function (Marris et al., 2020) or development (Sørhus et al., 2015). Moreover, some evidence suggests a reduced abundance of fish larvae proceeding the Deepwater Horizon oil-spill (Rooker et al., 2013), but few studies have reported effects at the population level (Fodrie et al., 2014; Ward et al., 2017). This apparent paradox can have many possible explanations, including biological processes, such as a dampening of effects by density-dependent survival (Ohlberger & Langangen, 2015). In addition, observational challenges, for example, limited knowledge of the environmental baseline (Joye, 2015), can make it difficult to detect impacts at the population level (Hjermann et al., 2007). Naturally caused mass mortality events can be considered part of the natural recruitment fluctuations. Hence, the population-level impact of naturally occurring mass mortality in the early life of fish can also be considered an impact of recruitment failure.

Here, we quantify the impact at the population level for a range of fish species from a mass mortality event at the early life stage and relate the impact to the life-history parameters of the species. Using both species-specific and stock-specific models, we ran two scenarios of early-life mass mortality, with 50% and 99% elevated mortality (Figure 1), and recorded the maximal loss in population-level biomass in the perturbed vs. unperturbed dynamics (referred to as impact). The recorded distribution of the between-year impact,

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characterized by the median (median impact) and 95th percentile (high impact), was related to life-history parameters such as natural mortality, degree of density dependence and recruitment variation.

2 | MATERIALS AND METHODS

First, we constructed a species-specific population model that accounts for important processes that can affect fish population-level responses to mass mortality events, including early-life density dependence, mortality, growth and inter-annual variation in recruitment. The species-specific model was parameterized for 40 different fish species based on empirical data to gain an understanding of how these factors may affect how early life mass mortality causes a reduction in population biomass. Second, we investigated detailed stage- and age-structured Bayesian state-space models developed specifically for three stocks, that is, the Barents Sea stocks of cod (*Gadus morhua*, Gadidae), haddock (*Melanogrammus aeglefinus*, Gadidae) and capelin (*Mallosus villosus*, Osmeridae, Figure S1). These stock-specific models, which were calibrated to high-quality data, account for a range of processes affecting the population dynamics going beyond the processes included in the species-specific models. These processes include egg production, intra-cohort density dependence, cannibalism, species interactions, age-specific harvesting and the effects of temperature. The three stock-specific models allow for assessing whether the lessons learned from the species-specific model hold when accounting for these more detailed processes.

2.1 | Species-specific model

To obtain a broad understanding of how mass mortality events affecting early life stages may propagate to the population, we applied a population dynamics model to a range of fish species (Figure 1). These species-specific models are simulation-based models that are

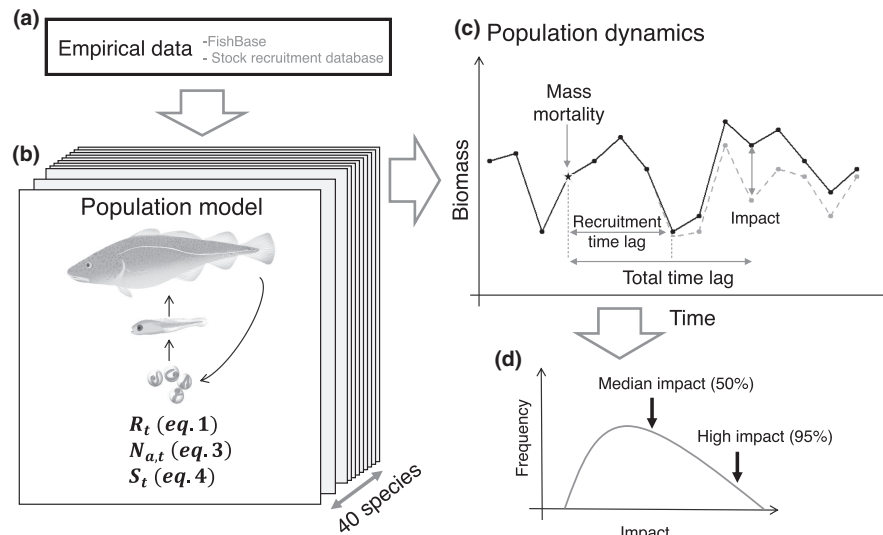


FIGURE 1 Illustration of the approach. Using empirical data from a range of fish species (a) a population model was constructed and parameterized (b). The population model was used to construct the population dynamics of each species (c, *black solid line*). To investigate how mass mortality events in early life may propagate to the population level, scenarios of mass mortality at the early life-stages in a single year were applied. The alternative population biomass trajectory (*dashed grey line*) was recorded and compared to the original trajectory. The impact, that is, highest percent reduction in biomass between unperturbed and perturbed time-series, appears with a time lag due to recruitment lag and growth lag before the affected year class reaches the maximal contribution to population biomass. The scenarios of mass mortality were applied to a range of years with contrasting population states, which provide a distribution of potential impacts at the population level (d, *grey solid line*). We recorded two metrics to reflect the impact distribution, the median and the 95th percentile, referred to as the median and high impact respectively.

parametrized partially based on fitting data and partially based on values obtained from the literature. More specifically, the model consists of two main components: (i) a stock-recruitment function and (ii) adult survival, growth and maturation. This model accounts for important processes, such as early-life density dependence in survival, interannual variation and autocorrelation in year-class strength, as well as growth and mortality (both natural and fishing-induced). The model was parameterized for 40 different fish species, based on two sources: for the stock-recruitment data, we relied on the original database of Ransom Myers (Myers et al., 1995), and for growth parameters, and values of natural mortality and age-at-maturity we relied on FishBase (Froese & Pauly, 2000).

The modern RAM Legacy Stock Assessment Database (Ricard et al., 2012) contains stock data based on assessments where the explicit form of the stock-recruitment relationship is included. Moreover, it has been shown that these assumptions can have profound effects on the recruitment time series (Dickey-Collas et al., 2015). To circumvent this problem, we used the original database of Ransom Myers (Myers et al., 1995), which was based on assessment models with fewer restrictive assumptions (Ricard et al., 2012). Here, we did not focus on a particular species or region but rather aimed for contrast in parameters of interest, that is, recruitment variation, degree of density dependence and natural mortality. As a result, we selected one stock per species based on a set of selection criteria. Following Foss Grant et al. (2016), we selected stocks with at least 10 years of data and orders with at least five species. When more than one time series was available, we selected the longest time series. Species for which the spawning

stocks were reported in numbers (not in weight) were removed from the analysis. This procedure made 43 fish species with stock-recruitment data for 10 years or more available. Capelin was not included in the initial selection, but because of the availability of a detailed state-space model for this species, capelin was added to the list of species. Of these 44 species, we were able to construct the population dynamics for 40 species. For four species, Blueback herring (*Alosa aestivialis*, Clupeidae), Norway pout (*Trisopterus esmarkii*, Gadidae), Spanish sardine (*Sardina pilchardus*, Clupeidae) and Sablefish (*Anoplopoma fimbria*, Anoplopomatidae), we were unable to obtain the population dynamics because of lacking data on growth for Blueback herring and because the populations went extinct for the available values of natural mortality, growth and age at maturity for Norway pout, Spanish sardine and Sablefish. The time-series data for recruits and spawners were standardized to thousands of recruits and tons of spawners and were doubled, assuming a 1:1 sex ratio, in the relatively few cases when only females were reported. The selected species covered a relatively large range of parameter values such as natural mortality and recruitment variation (Figure 2). A list of species included in the analysis is shown in Figure 3 and Table S1.

The species-specific models need a stock-recruitment relationship. For simplicity, we used a linearized Ricker model (Ricker, 1954) that was fitted to the data for each of the stocks using the software Just Another Gibbs Sampler (JAGS, Plummer, 2003):

$$\log\left(\frac{R_t}{S_t}\right) = \beta_0 + \beta_1 S_t + \epsilon_t \quad (1)$$

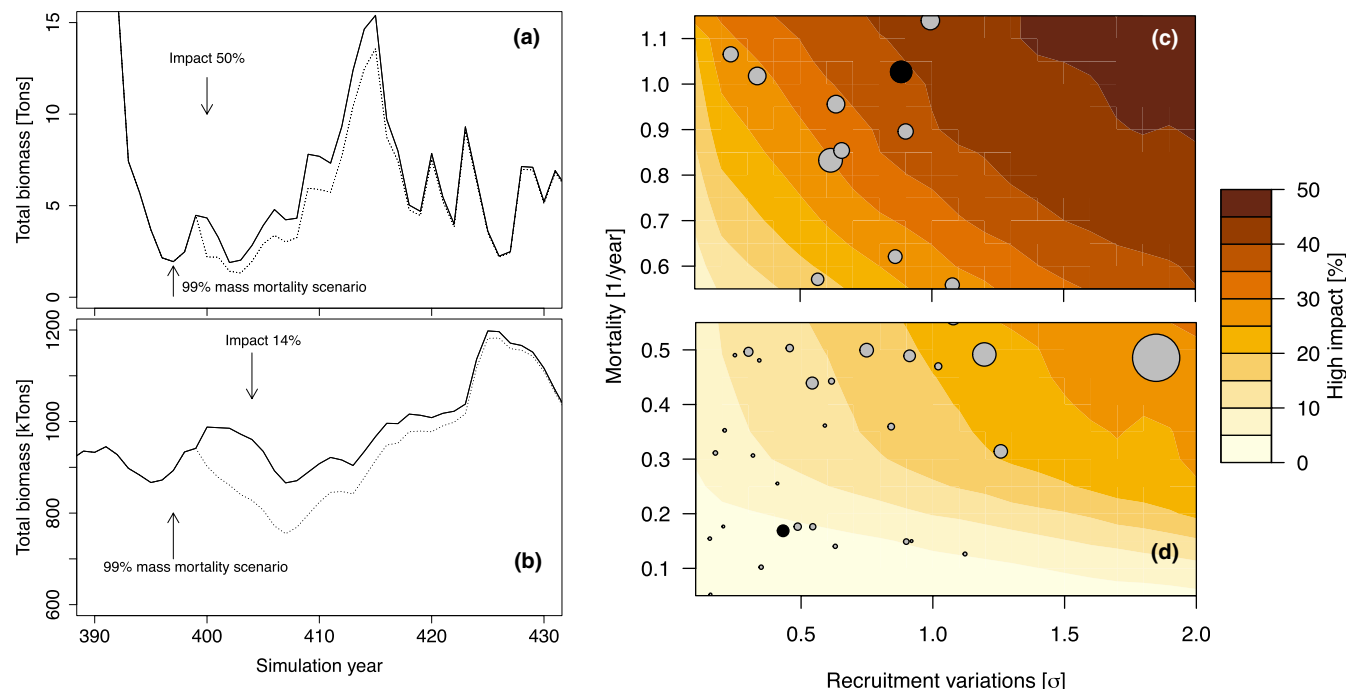


FIGURE 2 Impact of a 50% mass mortality event at the population level. Panels (a) and (b) show two examples (a, alewife and b, cod) of a mass mortality scenario in the simulated population dynamics. The unperturbed biomass is shown (*black lines*) as well as the alternative perturbed biomass (*dotted lines*). The resulting high impact (95 percentile impact, [Figure 1](#)) of a 50% mass mortality event across a range of values for recruitment variation and natural mortality is shown (panels c and d). This output was generated by the use of two sets of model parameters (Table S1), that is, one set for alewife (panel c) and one set for cod (panel d) to avoid extinction when extrapolating parameter values. For visual enhancement, the impact was smoothed using a convolution with a 3×3 kernel with 30% for the mid-point and uniform values for all other points using the `convolution()` function from the `OpenImageR` package in R (Mouselimis, 2022). The size of the filled circles indicates the strength of the impact of the species (see [Figure 3](#) for exact values). The black circles indicate cod (panel d) values and alewife (panel c) values. The high impact is generally larger with increasing recruitment variations and mortality.

where R_t and S_t are corresponding recruits and spawner biomass respectively (spawner biomass shifted with the number of years corresponding to the age at recruitment). β_0 and β_1 are constants representing density-independent and density-dependent effects. The ϵ_t is the error term, which we assumed to be autocorrelated with lag 1:

$$\epsilon_t = \varphi \epsilon_{t-1} + \omega_t \quad (2)$$

where φ is the coefficient of autocorrelation and ω_t is a normally distributed error with zero mean and standard deviation σ . For the population dynamics, we used the median estimated posterior parameter values. To account for the typically large stochastic component of the stock-recruitment relationship, we resampled the residuals (ω_t) in the species-specific model. More details on the data used and estimated parameter values are shown in the Supplementary Information (Table S1).

For each stock, we completed the life-cycle model by expanding the above defined stock-recruitment model with an age structured model that accounts for growth and mortality (natural + fishing mortality). Abundance at age was calculated from a standard cohort relationship:

$$N_{a,t} = \begin{cases} R_t & \text{for } a=r \\ N_{a-1,t-1} \exp(-(M+F)) & \text{for } a>r \end{cases} \quad (3)$$

where $N_{a,t}$ is the abundance at age a in year t , R_t is the recruitment in year t (obtained from the stock-recruitment model), r is the age at recruitment, M is the natural mortality and F is the fishing mortality. Recruitment was calculated from the stochastic stock-recruitment function as described above for a given spawning stock biomass (SSB). The SSB (denoted as S_t in the equations) was calculated as:

$$S_t = \sum_{a=a_{\text{mat}}}^{\text{max-age}} W_a \cdot N_{a,t} \quad (4)$$

where the `max_age`, the number of year classes included in the model was set to 50 (100 for Greenland halibut). This was deemed acceptable for most species, as the maximum age (t_{max}) was calculated to be 40 years or less for all species based on the Hoenig relationship (Hoenig, 1983) $t_{\text{max}} = \exp((1.46 - \ln(M))/1.01)$, except Greenland halibut, with a maximum calculated age of about 80 years. The SSB in the model was calculated from the abundance-at-age and weight-at-age for ages equal and above the age at maturity a_{mat} (assuming that all individuals mature at this age). Mean growth was assumed to follow a von Bertalanffy growth curve:

$$W_a = W_{\infty} (1 - \exp(-k(a - t_0)))^b \quad (5)$$

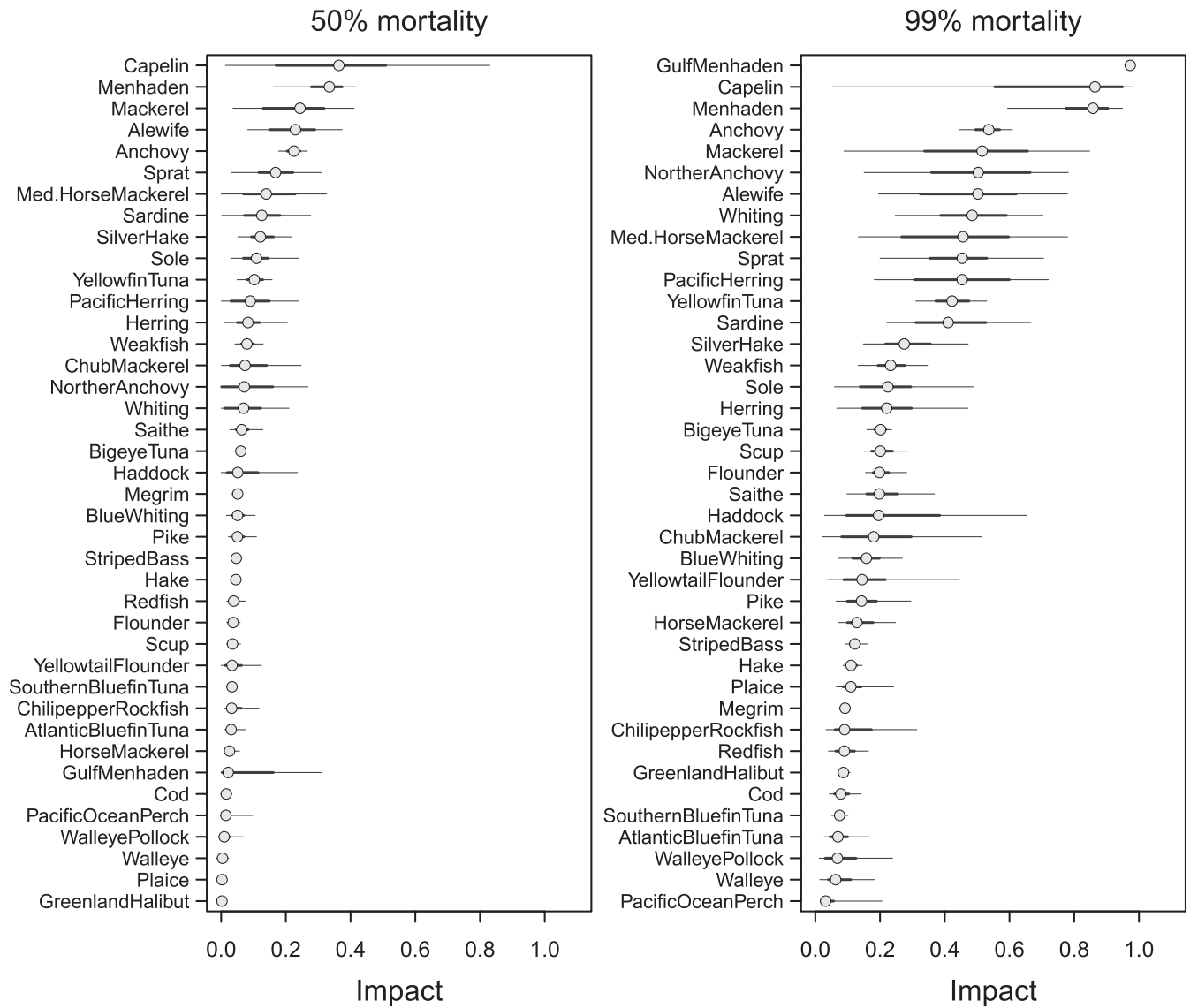


FIGURE 3 The impact distribution across species. The impact of the mass mortality scenarios for the 40 species sorted according to the highest median impact (*filled circles*) is shown. Moreover, the distribution of the impact is indicated with the 25% and 75% (*thick lines*) and 5% and 95% (*thin lines*) percentiles. Note that the right most thin lines correspond to the high impact used in the analysis. More information on scientific names and parameter values are shown in Table S1.

where W_a is the weight at age a , W_∞ is the asymptotic weight, k is the growth coefficient, t_0 scales the size at age zero and b is the power coefficient in the length–weight relationship.

The life-cycle models were supplemented with mortality, growth and maturity data from FishBase (Froese & Pauly, 2000). Because stock-specific data were not generally available, we used all available species-specific von Bertalanffy growth parameter values (asymptotic length L_∞ and k) and temperature (T) data to calculate an associated natural mortality (Pauly, 1980):

$$\ln M = -0.0066 - 0.279 \ln L_\infty + 0.6543 \ln k + 0.4634 \ln T \quad (6)$$

Based on these growth and natural mortality estimates, we used the median natural mortality and the associated growth data unless otherwise specified in Table S1. All reported age at maturity, a_{mat} ,

estimates were extracted and we used the rounded-down median reported value. Fishing mortality (F) was not in general known at the species level, and we used F to tune the modelled SSB to a comparable level to the observed median SSB (Figure S4). This was done by iteratively running the population dynamics for different levels of F and comparing the median simulated SSB with the median observed SSB. The F that minimized the difference between the median simulated and observed SSB was then used in the consecutive analysis. We tested with F values in steps of 0.01 year^{-1} up to 0.3 year^{-1} and in steps of 0.1 year^{-1} above that level up to a maximum of 3.0 year^{-1} . Sensitivity testing of the F values indicated that the exact values did not alter the main conclusions of this work (Supplementary Information and Figure S5). The species-specific population-level models were all run for 650 years by resampling the residuals from the stock-recruitment models for each year. The first 100 and the

last 50 years were discarded to minimize edge effects (Figure S4). The range of natural mortalities and recruitment variability is shown in Figure 2, and all parameters used for the population dynamics are shown in Table S1.

2.2 | Stock-specific population models

Dynamic life cycle models, such as stage-specific state-space models can be used to understand how perturbations at one stage may propagate to other stages and to the population-level (Maunder & Deriso, 2011). Such models are suitable to shed light on the effect of early-life mass mortality, but a certain degree of contrast in parameters that potentially have a strong influence on population dynamics, for example, the strength of density dependence, inter-annual variation in early-life survival and mortality (Ohlberger & Langangen, 2015) is needed to assess how mass mortality events impact populations with different life histories. The three stock-specific state-space models used in this study are a Northeast Arctic (NEA) cod (Ohlberger et al., 2014), a NEA haddock (Patin et al., 2016), and a Barents Sea capelin (Stige et al., 2018) model. The models were fit to stock-specific data including age- and stage-specific abundance (Figure S1) and weight as well as commercial data on landed fish (see, Ohlberger et al., 2014; Patin et al., 2016; Stige et al., 2018 for details). More details about the stage-specific state-space models are available in the Supplementary Information.

2.3 | Mass mortality scenarios

We ran mass mortality scenarios—a single year with 50% elevated mortality or a single year with 99% elevated mortality—for the early life stages (Figure 1) in both the species-specific and the stock-specific models. We used a hindcasting scenario approach similar to the method used by Ohlberger and Langangen (2015). In the species-specific model, this was done by scaling the SSB used in the stock-recruitment function. We applied the mortality scenario for each year from year 100 to year 600 in order to obtain a distribution of potential impacts.

For the stock-specific models, we applied the mortality at different stages for the three stocks to account for the difference in density dependence (SI). For the NEA cod, we applied mass mortality at the egg stage. For the NEA haddock, we applied the mass mortality event at the egg deposition stage (proxied by the SSB). In the haddock model, density dependence in survival was estimated to be relatively weak, while the opposite was true for the capelin model. For the Barents Sea capelin, it is uncertain whether the density dependence acts mainly during the spawning of eggs or later at the egg, larval and juvenile stages. As a result of the relatively strong density dependence in capelin, the exact timing of when density dependence acts are highly relevant for understanding how mass mortality propagates to the population level. To address this uncertainty, we ran two sets of scenarios for capelin. In the first scenario

group, we allowed mass mortality to affect the reproduction stage (by reducing the effect of SSB on juvenile recruitment). This means that we assumed that the mass mortality event occurred before the density-dependent regulation of cohort size. In the second group of scenarios, we allowed the mass mortality to directly affect the abundance of 0-group juveniles. This means that we assumed that the mass mortality event occurred after the density dependence.

Similar to the species-specific models, the impact at the population level in the stock-specific models was delayed and we did not include the last 10 years of the time series for cod and haddock and the last 5 years for capelin to minimize edge effects. This left us with 47 years of mass mortality impact scenarios for cod, 23 years for haddock, and 31 years for capelin. By including two scenarios, one with 50% elevated mortality and one with 99% elevated mortality, we covered the range of mortality levels considered to be mass mortality events (Mangel & Tier, 1994).

After the simulated mass mortality event, in both the species-specific model and the detailed stock-specific models, we followed the population dynamics and compared it to the unperturbed dynamics (Figure 1c). We recorded the highest percent reduction in population biomass (biomass of all individuals older than the recruitment age) between the perturbed and unperturbed time-series—named ‘impact’—and obtained a distribution of such impacts across different mass mortality event scenarios (Figure 1d). We then extracted two key metrics from the above distribution, that is, the median and high impact (Figure 1d) where high impact is defined as the 95th percentile of the impact distribution. Finally, we tested for an association between median and high impacts of the species-specific models with the underlying parameters, in particular, the mortality, recruitment variation and compensatory density dependence using Spearman's rank correlation tests. Moreover, quantile regression was performed using the *quantreg* package in R (Koenker, 2022). For illustrative purposes, we ran the scenarios for a range of combinations of mortality (M : 0.05–1.15 year⁻¹) and recruitment variation (σ : 0.1–2.0) for two example species combined (cod and alewife), keeping the other parameters fixed.

For comparison, we calculated the interannual percentage change in the SSB for the 40 species. This was done by calculating $\Delta_t = \frac{SSB_t - SSB_{t-1}}{SSB_{t-1}}$, from the time-series used in the species-specific model.

3 | RESULTS

3.1 | Species-specific model results

We obtained estimates of population-level impacts of 50% and 99% mortality events in the early life for the 40 species (Figures 2 and 3). The range of species included in the analysis provides a large contrast in parameters such as interannual variation in recruitment and natural mortality with large differences in population-level impacts (Figure 2). The median and high impacts of mass mortality events correlated positively with natural mortality (Figures 4 and S2) for

both 50% and 99% mass mortality events. The degree of density dependence correlated negatively with the median impact of a 50% mass mortality event, but not for the 99% mass mortality event (Figure 4). The degree of density dependence did not correlate significantly with the high impact for any of the mass mortality scenarios (Figure S2). We note that the significance of the correlations between the median impact of 50% mortality and density dependence was valid both when including all species and when species with overcompensation were excluded (cf. Figure 4). Recruitment variation correlated positively with the high impact, but not with the mean impact, for both mass mortality scenarios (Figures 4 and S2). The mean natural interannual percent change in the spawning stock biomass (SSB) for the 40 species varied between species but was typically in the range of 10%–50% with extremes of 4% and 63%.

3.2 | Stock-specific model results

For the detailed stock-specific models, the mass mortality events led to a reduction in biomass for all three modelled species. The impact distributions at the population level due to the mass mortality events are shown in Figure 5. For the 50% mass mortality, cod, haddock and capelin had a median impact of 8%, 9% and 22%, while the

high impact was 12%, 22% and 33% respectively (Figure 5). Similarly, for the 99% mass mortality scenario, cod, haddock and capelin had a median impact of 18%, 18% and 47% while the high impact was 34%, 47% and 69% for cod, haddock and capelin respectively (Figure 5). Results for an alternative scenario (see Section 2), where the mass mortality event was applied before the early-life density dependence in capelin indicated generally lower impacts (Figure S3).

4 | DISCUSSION

The early life of fish is typically associated with a very high natural mortality (Pepin, 2016) and chronic (small but persistent) changes in mortality are expected to have a larger effect on the amount of fish becoming adults (recruitment) compared to episodic events such as mass mortality events (Houde, 1989). Despite these general considerations, our results show that mass mortality events affecting the early life stages of fish can have important consequences at the population level (Figures 3 and 5). The mass mortality scenarios indicate that species with high mortality, that is, short-lived species and low compensatory density dependence in survival will have a larger median impact of a 50% mortality event. However, the high impact of a 50% mortality event is positively associated with the interannual

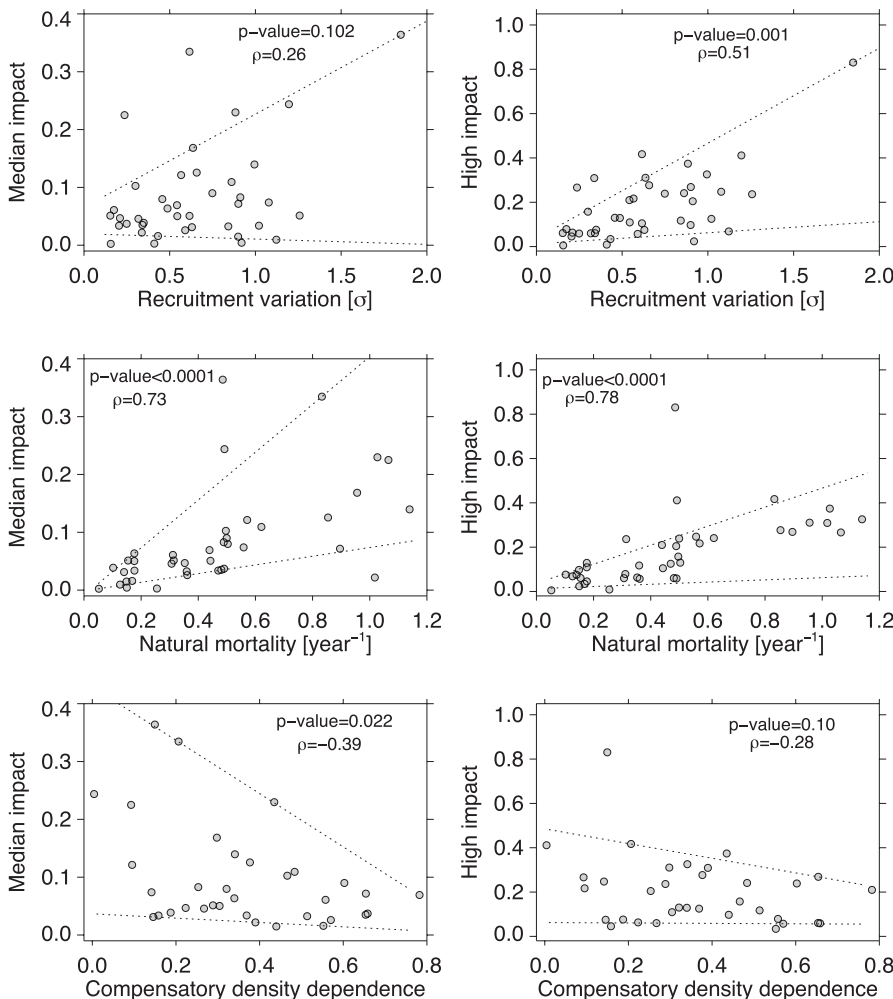


FIGURE 4 Relationship between impact and life-history parameters. The correlations between the median (left column) and high impact (right column) of a 50% mortality in the early life stages and recruitment variation (upper panels), natural mortality (middle panels) and density dependence (compensation at recruitment age of a 50% mortality at median SSB excluding overcompensation, lower panels) are shown. Correlation coefficients were calculated using Spearman rank correlation. The 10 and 90 linear percentile regression indicates the range of plausible impacts (dotted lines).

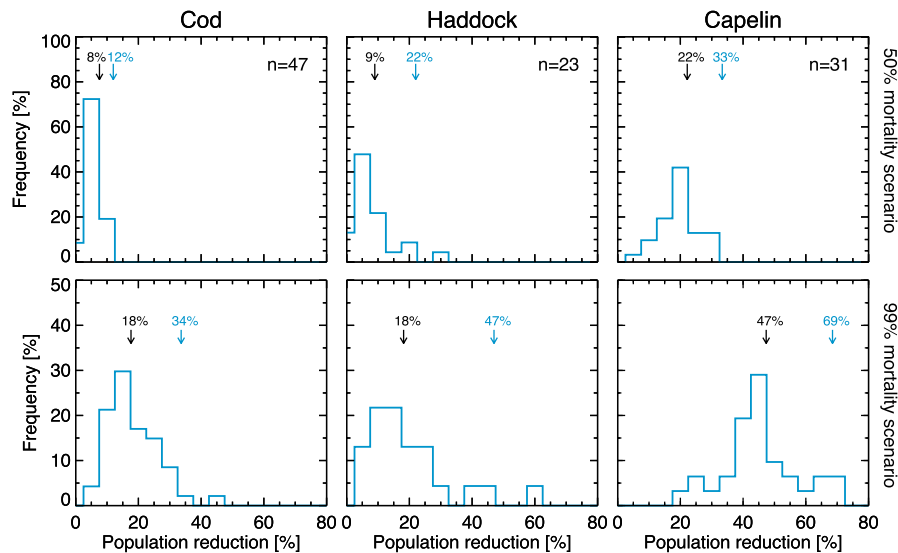


FIGURE 5 Impact distributions for the stock-specific models. The resulting distributions of population-level impacts (blue lines, number of individual years n) for the three stock-specific models, that is, cod (left panels), haddock (central panels) and capelin (right panels). The upper row shows the impact distributions for the scenarios of a 50% mortality event during the early life stage while the bottom row shows the distributions for the scenario of a 99% mortality event during the early life stage. The blue and black arrows indicate the high impact and median impact respectively (cf. Figure 1). The results for cod are obtained from the same simulations as in Ohlberger and Langangen (2015).

variation in recruitment but not significantly associated with density dependence (Figure 4). Moreover, we find that the massive 99% mortality event in early life is not significantly compensated by density dependence (Figure S2) for either the median or the high impacts. Such high mortality events leave few individuals to survive to later life stages, and density-dependent survival is typically not enough to significantly compensate for the loss cf. (Ohlberger & Langangen, 2015). Similar patterns were found also when we applied the mass mortality scenarios to the stock-specific models. We found slightly higher median impacts at the population level for haddock compared to cod for a 50% mass mortality event during early life (Figure 5). This may be because the higher fishing mortality in cod is balanced by stronger density dependence (Ohlberger et al., 2014) compared to haddock (Patin et al., 2016). The impact of a mass mortality event affecting early life stages is exacerbated by high fishing mortality but dampened by compensatory density dependence later in life.

Moreover, we found that the high impact of a 50% mass mortality was higher for haddock (22%) compared to cod (12%, Figure 5). This can be explained by the generally large inter-annual variability in the haddock recruitment (Friedland, 2021), which is often referred to as pulsed recruitment. For the 99% mass mortality events during early life, the median impact at the population level was the same for cod and haddock. For the relatively short-lived capelin, we detected a higher overall impact of mortality events when these were applied after the early life stages with density-dependent survival (Figure 5) compared to when they were applied before density-dependent population processes (Figure S3). Moreover, both the median and high impacts were generally higher for capelin than cod and haddock, as expected for a shorter-lived species.

Our estimates of population-level impacts of mass mortality events in the early life of fish can be compared to reported

mass mortality events in fish. For example, the bloom of the algae *Chrysochromulina polylepis* along the coast of Skagerrak in 1988 caused high mortality (about 60%) in juvenile cod (Chan et al., 2003). Despite the high mortality, the system mostly recovered 1 year after the event (Chan et al., 2003; Gjøsaeter et al., 2000). The cod model applied in this study was not specifically tailored for the cod population in the Skagerrak. Nevertheless, we note that our model predictions are generally consistent with the reports from the bloom in Skagerrak in 1988, with low effect at the population level of a mortality event of both 50% (less than 4%) and 99% (less than 15%).

More recently, an extreme heat wave in the North Pacific in 2014–2016 caused high mortality in fish. In particular, in 2015 the early life stages of the Gulf of Alaska walleye pollock (*Gadus chalcogrammus*) suffered very high mortality and the year class almost completely disappeared (Rogers et al., 2021). At the population level, the abundance of walleye pollock was reduced by about 70% between 2015 and 2017 (Barbeaux et al., 2020). In contrast, for walleye pollock, we found a reduction in biomass at the population level of up to 24% caused by the nearly full loss of a year class. Our result seems lower than the reported reduction despite intrinsic differences between abundance and biomass. However, we note that the heatwave lasted for more than 1 year and that the resulting increase in mortality was also affecting adult fish.

Another example of mass mortality events is industrial accidents such as oil spills, for example, Exxon Valdez and Deepwater horizon accidents (Crone & Tolstoy, 2010; Peterson et al., 2003). Despite the well-documented lethal effects of oil components on the early life of fish, few studies have reported population-level impacts of such events (Fodrie et al., 2014; Ward et al., 2017). Our results offer a potential explanation, for why acute fish mortality at the early life stages from oil spills is difficult to observe at the population level.

First, the effects at the population level are often substantially larger for the high impacts (i.e. the tail of the distribution) compared to median impacts (Figure 3), indicating that for the same fish species large population-level effects will only occur sporadically. Second, the natural variation in biomass in the unperturbed population is typically at the same level or higher (10%–50%) than the estimated impacts of the 50% mass mortality scenarios (typically less than 25%, Figure 3), making it potentially difficult to detect.

While it is difficult to predict the effects of potential oil spills at the cohort level of these fishes, examples of detailed studies using oil-spill modelling combined with biological drift models for cod, indicate maximally elevated mortality of about 43% (Carroll et al., 2018; Vikebø et al., 2014), comparable to the 50% mortality scenario in the present study. Similarly, a field study of several fish populations following the Deep Water Horizon accident found relatively weak effects at the cohort level (Rooker et al., 2013). We argue that detailed system-specific studies are needed to fully understand the effects of oil spills on fish populations. However, our results enable general predictions of which species are more vulnerable to large population-level impacts and hence would potentially warrant more attention to better understand how oil spills may affect fish populations (Figures 2 and 4). Our results furthermore provide a first approximation of how the population-level effects depend on the magnitude of the mass mortality event and the species' life history (Figures 4 and S2). Despite the limited observation of the population-level impact of oil spills on fish, our results indicate that there is indeed the potential for a considerable population-level effect, typically up to the range of about 25% reduction in total population biomass, depending on species (Figures 2–4). The difficulties of detecting surprising events, that is, large die-offs or unexpected increases, in the time series of population abundance were also pointed out by Anderson et al. (2017). They investigated the population dynamics of more than 600 species and found that surprising events (black swan events) occurred in about 4% of the time series, with such extremes being less often detected in fish species.

We note that there are a few extreme impacts, especially when considering the high impacts, that were in part caused by very high estimated fishing mortality. These species will typically be dominated by a single cohort. A mass mortality event affecting this specific cohort will propagate over the years reducing future recruitment, which in part may explain the observed extreme impacts. Moreover, we note that the species-specific model predicted a higher impact for capelin than the stock-specific model. For cod, the species-specific model predicted lower impacts compared to the stock-specific model, while for haddock the predictions of the two models were more consistent (Figures 3 and 5). We interpret this as an indication that the species-specific models are sometimes less accurate for the individual species, but we argue that the overall patterns are reliable. In general, our results follow predictions from life-history theory, for example, long-lived species are expected to be less sensitive to changes in reproduction compared to short-lived species (Durant & Hjermann, 2017; Stearns, 1992). The species data used in this analysis cover several taxa and a range of life histories.

However, the species are not randomly selected and are biased, for instance towards commercially valuable species, and do not cover the full spectrum of, for example, recruitment variation and natural mortality (Figure 2). Moreover, interannual variation in natural mortality and in growth is not taken into account in the species-specific model, which also assumes equal biomass of males and females in the few cases where only female biomass is reported. Furthermore, the model does not include species interactions and indirect effects of mass mortality that can potentially be large (Langangen, Ohlberger, et al., 2017). Despite such limitations, we have clearly demonstrated the importance of natural mortality, density dependence, and variation in year-class strength in shaping the population-level impact of mass mortality during early life stages. These general relationships allow for quantitative predictions of the range of potential impacts of early-life mass mortality in a large range of fish species. Such quantitative predictions will potentially be useful in the face of the rising occurrence of mass mortality events across the globe.

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DATA AVAILABILITY STATEMENT

Data sets for this research are included in Myers et al. (1995) and Fishbase.

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